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Direct fire-induced reptile mortality in the Sierra Morelos natural protected area (Mexico)

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Abstract

Little is known about fire as an agent of direct animal mortality, and specifically, there is controversy regarding the effects of fire on reptiles. In the Sierra Morelos natural protected area in Mexico, both unplanned (e.g., man-made illegal and accidental burns) and prescribed burns occur during the dry season. In this study, we assessed direct fire-induced reptile mortality in the Sierra Morelos natural protected area by comparing live and dead individuals. Of the 14 reptile species reported in the area, seven were found dead due to fire. One-third of the individuals found in 2021 (34% of 169 ind.) and 2022 (33% of 33 ind.) were killed by fire. The mean density of detected dead individuals was 1.60 ± 2.99 individuals/ha in 2021 and 0.31 ± 0.27 individuals/ha in 2022. Mortality densities were similar in areas subjected to prescribed burns and in areas affected by unplanned burns ($W = 37.5$, $p = 0.4383$). Since our survey likely underestimated the actual mortality caused by fire, our findings show the important direct impact of fire on the reptile community of the Sierra Morelos natural protected area and support the notion that anthropogenic fire can represent a serious risk for reptiles in fragile ecosystems.

Key Words

carcass count, fire impact, fire management, prescribed burning

Introduction

Fire is a fundamental ecological process in many ecosystems and shapes their structure, composition, and function (Bond and Keeley 2005; Bowman et al. 2009; Pausas and Keeley 2009; He et al. 2019; McLauchlan et al. 2020). Some species are adapted to natural fire regimes (Keeley et al. 2011; Pausas and Parr 2018) and can benefit from fire and the environmental heterogeneity it creates (Parr and Andersen 2006; He et al. 2019). People have used fire to modify environments for millennia (Bowman et al. 2011); however, human activities are now changing patterns of fire at a global scale (Kelly et al. 2020; Bowman et al. 2020). Extreme droughts have increased the frequency, duration, and intensity of fires in many regions of the world due to human-induced climate change, and ecosystems worldwide are becoming more stressed due to warmer climates (Duane et al. 2021). The fire season has lengthened for 25.3% of the Earth's vegetated surfaces, leading to an increase in the intensity and frequency of wildfires and an unprecedented amount of burned area (Jolly et al. 2015; Duane et al. 2021; Garcia et al. 2021). These changes in fire regimes are changing the biodiversity patterns of local communities (McKenzie et al. 2004;

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Duane et al. 2021) and threatening species with extinction across the globe (Kelly et al. 2020).

Fire can affect species populations through direct and indirect effects (Whelan 2002; Engstrom 2010). The direct effects of fire include mortality during a fire event (Whelan 2002; Smith et al. 2012; Jordaan et al. 2020; Tomas et al. 2021) due to smoke inhalation (Lyet et al. 2009; Jordaan et al. 2020), radiant heat, or direct consumption by flames (Jolly et al. 2022). The indirect effects of fire are related to changes in habitat suitability in recently burned areas, such as reductions in food and shelter, which may increase species susceptibility to predation (Conner et al. 2011; Leahy et al. 2016; Santos et al. 2022); alteration of microclimatic conditions, which may increase overheating risk (Legge et al. 2008; Ferreira et al. 2016a); or threats related to the successional dynamics that fire initiates (Whelan 2002; Engstrom 2010). Species survival to fire events depends on functional traits (Santos et al. 2016), such as dispersal ability, size, microhabitat preference or evolutionary exposure to fire, and adaptation to local fire regimes (Santos and Cheylan 2013; Pausas and Parr 2018; Nimmo et al. 2021; Jolly et al. 2022). Vertebrates that disperse over large expanses, such as birds and large mammals, are often less vulnerable to direct mortality caused by fire, whereas most herpetofaunal species have more limited abilities to evade fire (Greenberg et al. 2018). Additionally, physical conditions such as age, reproductive status, fat reserves, or ecdysis may increase individuals' susceptibility to direct fire effects (Nimmo et al. 2021; Jordaan and Steyl 2023).

There is controversy regarding the effects of fire on reptiles; some studies have reported positive effects of fire on reptile communities (Langford et al. 2007). For example, it has been suggested that fire can temporally increase nutrient availability or stimulate seed release in some plant species, leading to an increase in arthropods, which may benefit insectivorous reptiles (Pausas and Parr 2018; Smith 2018), or that fire can create open areas with better thermal quality for reptiles (Bury 2004). Most importantly, some authors suggest that direct negative impacts of fire are negligible for reptiles (Means and Campbell 1981; Ford et al. 1999; Russell et al. 1999; Greenberg and Waldrop 2008), especially low-intensity fires (Floyd et al. 2002; Costa et al. 2013; Jolly et al. 2022), and that direct mortality of herpetofauna from prescribed burns is rare (Harper et al. 2016; Greenberg et al. 2018; Certini et al. 2021).

On the other hand, many studies report important negative effects of fire on reptiles. For example, Popgeorgiev (2008), Smith et al. (2012), Tomas et al. (2021), Santos et al. (2022), and Ballouard et al. (2023) reported high direct mortality due to natural/unplanned fires, whereas Lyet et al. (2009), Cross (2015), and Jordaan et al. (2020) reported high direct mortality in prescribed burns. Popgeorgiev and Kornilev (2009) reported a lower abundance of four reptile species in burned areas than in unburned adjacent areas. McLeod and Gates (1998), Valentine and Schwarzkopf (2009), and Santos and Cheylan (2013) reported lower reptile abundance and diversity in frequently burned areas, while Santos and Poquet (2010), Abom and Schwarzkopf (2016), and Ferreira (2016b) reported changes in community composition with frequent fires, even in extremely fire-prone ecosystems such as those found in Australia, Argentina, the Iberian Peninsula, South Africa, and USA. Most of these assertions about the impacts of fire on reptile populations have been assessed based on changes in animal population size before and after fire and do not distinguish between survival/mortality and immigration/emigration, creating uncertainty regarding the proportion of animals that survived the passage of fire (Jolly et al. 2022). In fact, there is surprisingly little knowledge of fire as an agent of direct animal mortality (Nimmo et al. 2021; Tomas et al. 2021; Jolly et al. 2022). Systematic searches for carcasses after fires (Popgeorgiev 2008; Jordaan et al. 2020; Tomas et al. 2021; Ballouard et al. 2023) can enhance our understanding of the direct impact of fire on animal populations. This approach can aid in determining the most suitable fire management practices for wildlife conservation in various ecosystems.

In Mexico, approximately 90% of recorded fires have anthropogenic causes (Trejo 2008). This is particularly concerning due to the increasingly warm and dry conditions in the context of a country highly vulnerable to climate change (Seager et al. 2009). The natural protected area of Sierra Morelos State Park (PESM by its acronym in Spanish) represents 78% of the green areas within Toluca city (Gobierno del Estado de México 2013), comprising major habitats for resident and migratory wildlife. The PESM contains a great diversity of vertebrate species, including at least 12 mammals, 184 birds, 14 reptiles, and two amphibians (www.inaturalist.org). In the PESM, many fires occur every dry season. However, some of them are prescribed burns conducted as part of the natural protected area management program. This paper focuses on estimating the death toll among reptiles directly caused by fires based on data collected in the field by accounting for live and dead individuals.

Materials and methods

Study site

The PESM is located north of Toluca city (19°20'00"N–19°17'47"N, 99°39'00"W–99°43'25"W), approximately 63 kilometers southwest of Mexico City (Fig. 1). The PESM ranges in elevation from 2,630 to 3,040 m above sea level (Sierra-Domínguez et al. 2018). The dominant climate is temperate subhumid, with summer rains. The dry season spans from November to May, and the rainy season spans from June to the end of October. The average annual rainfall from the nearest weather station (located less than 1 km away in the community of Calixtlahuaca) is 840 mm. The wettest month is July, with 167 mm of rain, whereas the driest month is December, with 9.6 mm of rain. Due to the high elevation, daily temperature fluctuations are very pronounced throughout the year. The annual average temperature oscillates between 4.9 and 22.3 °C (Servicio Meteorológico Nacional 2021).

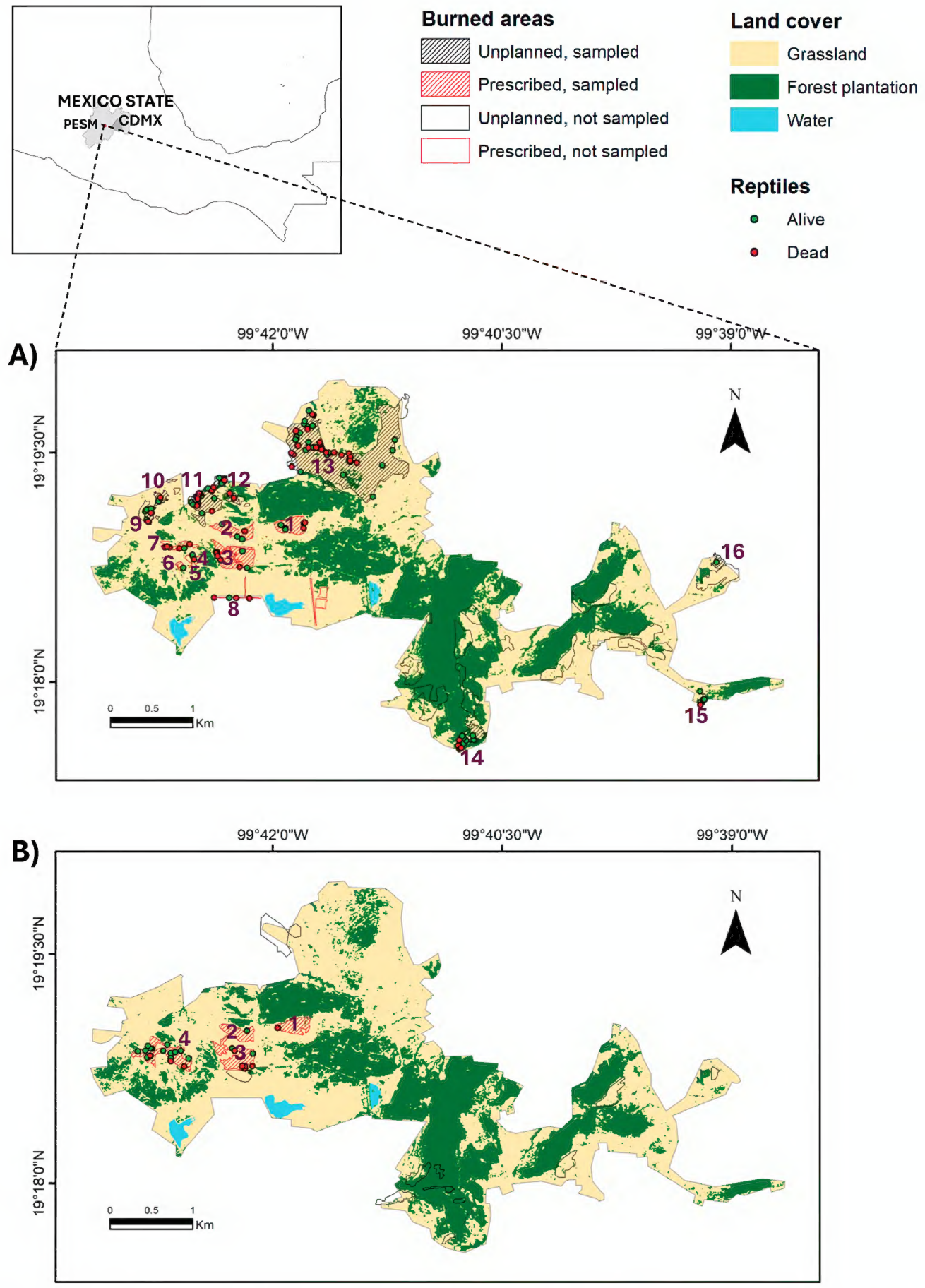

Figure 1. Burned areas in the PESM during the dry season in 2021 (**A**) and 2022 (**B**) and the reptiles found within them. The burned areas surveyed (marked with stripes) were delineated in the field with GPS and were used to calculate the density of dead and live reptiles. The burned areas not surveyed (without stripes) were delineated using satellite images. Red areas were prescribed burn sites as part of a fire management program in the natural protected area, whereas black areas were burned for reasons unrelated to the fire management program.

PESM was declared a natural protected area in 1976 with an original extent of 394.96 ha (Gobierno del Estado de México 1976). In 1981, an additional area of 860.13 ha was incorporated into the park (Gobierno del Estado de México 1981), reaching 1,255 ha. When the natural protected area was originally declared, approximately 12.65 ha of human settlements (isolated buildings separated by cultivated terraces and backyards) were already present within the polygon. Since that time, the urban built-up area has expanded in the PESM as cultivated land and backyards were replaced by new buildings (Sierra-Domínguez et al. 2018).

The current landscape of the PESM consists of a small plain and multiple hills covering the municipalities of Toluca (98% of the PESM) and Zinacantepec (2%) (Olvera-Viscaino 2018). The hills originated during the Miocene and are formed by highly permeable volcanic rocks that favor water infiltration (Niño-Gutiérrez et al. 2007), thus playing an important hydrological role. In contrast, the soil composition of the plain has a high clay content, which favors the flooding of the land during the rainy season and the formation of lagoons. Most of the PESM is covered by grassland and shrubland ecosystems. The forest cover is composed of introduced species that form forest stands, mainly *Cupressus lusitanica*, *Eucalyptus* sp., and *Pinus radiata*, which are considered fire-prone species, particularly the latter two (McWethy et al. 2018). There are also native tree species in the area, such as *Buddleja cordata*, *B. microphylla*, wild black cherry (*Prunus serotina*), Mexican hawthorn (*Crataegus mexi-*

cana), shrub oaks (such as *Quercus frutex*), and arboreal oaks (*Q. mexicana* and *rugosa*), but they mostly grow isolated rather than as forest stands, with the exception of shrub oaks (Sierra-Domínguez et al. 2018). Scientific information about the biodiversity of Sierra Morelos is scarce; to date, the records published in iNaturalist probably constitute the most reliable information on diversity in PESM and consist of 441 species of plants, 62 fungi, 542 arthropods, and 213 vertebrates. Fourteen reptile species have been reported in the area.

Study species

Of the 14 species reported for the PESM, five belong to the genus *Thamnophis* (Garter snakes, Colubridae family). The most common *Thamnophis* species in the PESM are *T. scaliger* (adult snout-vent length, SVL of 29–38 cm), *T. eques* (adult SVL of 39.5–92 cm), and *T. scalaris* (adult SVL of 34.5–50 cm) (Reguera et al. 2011; Manjarrez et al. 2007, 2014). They are slow-moving, and ground-dwelling species that can usually be found in grasslands and can use natural cavities or burrows on the ground. The lined Toluca earth snake (*Conopsis lineata*) is also a ground-dwelling snake from the Colubridae family that can be found in grasslands and forests (Sunny et al. 2023), usually under rocks. The Mexican dusky rattlesnake (*Crotalus triseriatus*) is also present in the area (Sunny et al. 2019; Rubio-Blanco et al. 2024) and can usually be found in bunchgrass, such as *Muhlenbergia* sp. Four reptile species present in the PESM belong to the *Sceloporus* genus (Phrynosomatidae family); the most common is the torquate lizard (*S. torquatus*), a lapidicolous species with an adult SVL of 8.4 to 9.7 (Ortiz et al. 2001). The graphic spiny lizard (*S. grammicus*) is smaller and much less abundant in the area and can usually be found in fallen logs. The Mexican plateau horned lizard (*Phrynosoma orbiculare*, also from the Phrynosomatidae family) is a lizard that typically reaches an adult SVL of 6.5 to 8.5 cm (Hernández-Navarrete 2018). This species is classified as threatened in Mexico under NOM-059-SEMARNAT-2010 and inhabits open areas and grasslands, using bunchgrass for perching and shelter (Gómez-Benítez et al. 2021). The transvolcanic alligator lizard (*Barisia imbricata*), which belongs to the Anguidae family, has adults with SVLs ranging from 9.38 to 9.7 cm (Woolrich-Piña et al. 2021). It is a ground-dwelling species commonly found among bunchgrasses (Sunny et al. 2017).

Methodology

The methodology consisted of mapping the burned areas in 2021 and 2022 within the PESM and searching on the ground for live and dead reptiles throughout the entire extent of the burned areas after the fires occurred.

Assessing burned areas:

We sampled burned areas shortly after the fires occurred (from the same day up to three weeks; see Table 1). To assess the surveyed area, we recorded the perimeter of the sampled areas using GPS. Unburned areas within the burned area polygon were also registered and excluded. The area of the surveyed polygons was calculated using a Geographic Information System in UTM Zone 14 N, WGS84. To map all the other burned areas that we could not survey, Sentinel-2 satellite images were acquired at the end of the dry season in 2021 and 2022. We displayed

Table 1. Burned areas surveyed (prescribed or unplanned) identified according to Fig. 1, number of dead and live reptiles found, area burned, time between the fire and the survey (during the first week, second week, or third week), perimeter, and relationship between area and perimeter (fire shape) for each burned area surveyed.

Burned area id	Prescribed/Unplanned	Dead	Alive	Area (ha)	Dead/ha	Survey after fire	Perimeter (km)	Fire shape
1 (2021)	Prescribed	2	4	5.88	0.34	Third week	1.01	5.80
2 (2021)	Prescribed	1	3	5.41	0.18	Third week	1.47	3.68
3 (2021)	Prescribed	5	3	9.16	0.55	Second week	3.97	2.31
4 (2021)	Prescribed	1	1	0.29	3.43	Second week	0.24	1.20
5 (2021)	Prescribed	0	0	0.05	0.00	Second week	0.10	0.55
6 (2021)	Prescribed	0	1	0.67	0.00	First week	0.44	1.53
7 (2021)	Prescribed	5	3	2.01	2.49	First week	0.84	2.40
8 (2021)	Prescribed	3	1	0.24	12.26	Second week	1.66	0.15
9 (2021)	Unplanned	2	2	1.55	1.29	First week	0.57	2.70
10 (2021)	Unplanned	1	3	1.84	0.54	Second week	1.03	1.79
11 (2021)	Unplanned	10	15	10.38	0.96	Second week and third week	2.68	3.87
12 (2021)	Unplanned	2	3	1.65	1.21	First week	0.60	2.75
13 (2021)	Unplanned	20	46	73.73	0.27	First, second and third week	6.10	12.08
14 (2021)	Unplanned	5	19	5.11	0.98	First week	1.41	3.64
15 (2021)	Unplanned	1	5	0.91	1.09	First week	0.57	1.61
16 (2021)	Unplanned	0	2	1.71	0.00	First week	0.78	2.19
1 (2022)	Prescribed	1	1	5.49	0.18	First week	1.34	4.10
2 (2022)	Prescribed	0	2	4.76	0.00	First week	1.10	4.31
3 (2022)	Prescribed	5	2	9.16	0.55	First week	2.34	3.91
4 (2022)	Prescribed	5	17	9.53	0.52	Second week	3.01	3.17

the images in RGB colors in a Geographic Information System with the following band combinations: short-wave infrared (band 12: R), near-infrared (band 8: G), and green (band 3: B). We visually outlined the burned areas and calculated their extent. While we knew when the fire occurred at some sites, for others, the timing was uncertain. Thus, we used the Sentinel-2 satellite images to approximate the dates of the fires in cases of uncertainty. This approach allowed us to determine the time between the fire and the sampling.

Prescribed burned areas (conducted as a fire management program of the PESM) were differentiated from unplanned burned areas (e.g., man-made illegal or accidental burns) because the former were very similar in shape, extent, and location both years. In addition, we corroborated prescribed burns with local people and with the authorities of the PESM. The main objective of these prescribed burning practices was to preserve areas planted with non-native trees. While prescribed burning practices have been conducted in the PESM since at least 2013, in 2021 and 2022, the amount of burned area under this type of management increased considerably (from an average of 2.65 ha per year between 2013 and 2020 to 35.9 ha in 2021).

Searching for reptiles

We carried out the surveys from the end of January to the beginning of April 2021 and in January 2022 between 09:30 h and 15:00 h (except on one occasion when the fire started as we were leaving, and we stayed to extinguish it and survey the burned area at approximately 16:00 h). The sampling was conducted on sunny days, which are most common during the dry season. Since most fires occurred in grasslands, the majority of the surveys were conducted in this ecosystem. Only sites 12 and 14 were extensively covered by trees (cedars and eucalyptus, respectively).

Usually, during the first two weeks following a fire (but in some cases, up to three weeks), we sampled the entire burned area in search of reptiles. The burned area was divided among two to four people with experience in surveying herpetofauna. We walked across the entire area in a zigzag pattern, maintaining a distance of approximately two meters between passes to ensure that no areas were overlooked. In large burned areas, we needed to conduct surveys over several days. In 2021, the surveys were conducted over 18 days (approximately 100 hours; equivalent to 300 person-hours), and in 2022, they were conducted over four days (approximately 22 hours; equivalent to 66 person-hours).

When we found a reptile in the burned area, we identified the species, noted whether it was dead or alive, took a photograph, recorded the coordinates using GPS, and documented the type of habitat where it was found. When possible, we displaced live and/or dead individuals outside the burned area to avoid counting them twice. Carcasses were not collected because they represent a food resource for predators. Live animals were released near the edges of burned areas so that they could avoid short- and medium-term fire effects but could eventually return to the area. When needed, we poured clean water over the survivors to cool them and remove the ashes. The density of carcasses was obtained by dividing the number of carcasses by the area surveyed (the area recorded with GPS). Animals that died from a cause other than fire were excluded from the analyses and tables presented here. For example, one *Sceloporus torquatus* and one *Thamnophis* sp. were excluded because they seemed to have been crushed.

We conducted a Mann-Whitney U test to compare the density of dead individuals in prescribed burned areas versus unplanned burned areas. Finally, we assessed the relationship between the density of dead reptiles and burn shape (area/perimeter).

Results

During the 2021 dry season, 196.91 ha were affected by fire in the PESM (Table 2). Of these, 35.9 ha were prescribed burns, according to PROBOSQUE (a decentralized public entity from the State of Mexico affiliated with the Ministry of Agriculture; see Suppl. material 1), and occurred during the last half of January. The area sampled consisted of 120.60 ha and was divided into 16 sampling sites (23.72 ha in prescribed burned areas, with 8 sampling sites; Fig. 1A). In 2022, 63.33 ha were affected by fires in the natural protected area (Table 2). From this total, at least 28.95 ha, where we conducted our search (four sampling sites, Fig. 1B), were in prescribed burned areas, where the fire occurred on January 27th.

Table 2. Total burned area (ha), sampled area, prescribed burning area reported by authorities, and prescribed burning sampled area for 2021 and 2022 in the PESM.

	2021	2022
Total burned area (ha)	196.91	63.33
Sampled area (ha)	120.60	28.95
Prescribed burning area reported by authorities (ha)	35.9	No Data
Prescribed burning sampled area (ha)	23.72	28.95

Of the 14 reptile species reported for the PESM in iNaturalist (with research grade quality), we found nine (dead or alive) in the burned areas sampled: three garter snake species (*Thamnophis eques*, *T. scalaris*, and *T. scaliger*), the Mexican plateau horned lizard (*Phrynosoma orbiculare*), the torquate lizard (*Sceloporus torquatus*), the graphic spiny lizard (*S. grammicus*), the Mexican dusky rattlesnake (*Crotalus triseriatus*), the transvolcanic alligator lizard (*Barisia imbricata*), and the lined Toluca earth snake (*Conopsis lineata*). Two of the missing species belong to the genus *Sceloporus* and have been reported only once for the PESM. Another missing species is *T. melanogaster*,

which is highly associated with aquatic habitats. *Thamnophis* species were classified only at the genus level due to the inability to distinguish the species of some burned carcasses. Of the 14 species reported for the PESM, seven were found dead by fire (Figs 2, 3, Suppl. material 2).

One-third of the individuals found in 2021 (34% of 169 ind.) and in 2022 (33% of 33 ind.) were killed by fire (Table 3). The overall mortality density (total dead individuals across the total sampled area) was 0.48 ind./ha (mean density ± SD = 1.60 ind./ha ± 2.99) for 2021 and 0.38 ind./ha for 2022 (mean = 0.31 ind./ha ± 0.27). In 2021, site 8 had the highest mortality density (12.26 ind./ha), and in 2022, site 3 had the highest mortality density (0.55 ind./ha) (Table 1). The mortality density in prescribed burned areas during 2021 was 0.72 reptiles/ha (mean = 2.41 ind./ha ± 4.18), whereas in unplanned burned areas during 2021, it was 0.42 reptiles/ha (mean = 0.79 ind./ha ± 0.47). During 2022, all the surveys were carried out in a prescribed burned area, where the mortality density was 0.38 ind./ha (mean = 0.31 ind./ha ± 0.27) (Table 3, Fig. 4). In 2021, 53% of the reptiles found in the prescribed burned areas surveyed were dead, whereas 30% of those found in unplanned burned areas were dead. In 2022, 33% of the reptiles found in prescribed burned areas were dead (Fig. 4). We found no significant differences in the densities of dead individuals between unplanned and prescribed burned areas ($W = 37.5$, $p = 0.4383$). We did not find a significant relationship between the density of dead reptiles and area/perimeter ($R^2 = 0.0528$, p value = 0.168).

In 2021, 84% of the carcasses were found on burned grass, 9% on leaf litter, 5% on rocky surfaces, and 2% on bare soil, whereas 35% of the survivors were found on burned grass, 25% on rocky surfaces, 11% on bare soil, 10% in/under agave plants, 8% on leaf litter, 6% in burrows, and 5% in fallen logs. One surviving *P. orbiculare* was found in a bird's nest on the burned grass. The taxa with a higher density of carcasses were *P. orbiculare*, with 0.17 dead ind./ha (mean = 0.30 dead ind./ha ± 0.51), and *Thamnophis* sp., with 0.16 dead ind./ha (mean = 0.84 dead ind./ha ± 3.05) (Table 3). The most common species found alive was *S. torquatus*, with 61 individuals, and *P. orbiculare*, with 24 (four of which were visibly injured). On two occasions, we arrived at the fire site while it was still burning and successfully prevented some animals (three *P. orbiculare*) from entering the fire. In 2022, all carcasses were found on burned grass, while 58% of the survivors were found on burned grass, 32% on a rocky surface, and 11% on bare soil. The species with the highest density of carcasses was *P. orbiculare*, with 0.14 dead individuals/ha (mean = 0.13 ± 0.09). The most common species found alive was *P. orbiculare*, with 11 individuals (two of them visibly injured).

Discussion

In this study, we assessed direct fire-induced reptile mortality in the Sierra Morelos natural protected area by comparing live and dead individuals.

Percentages of dead and live reptiles

A substantial proportion (more than 30%) of all reptiles found in burned areas between 2021 and 2022 were dead. Although the surveys were conducted on sunny days, minor changes in climatic conditions during the samplings should be considered a potential source of bias in the relationship between live and dead animals. Additionally, our findings should be interpreted with caution, as some carcasses may have been eaten by predators/scavengers, and some survivors may have abandoned the site, especially fast-moving species such as *S. torquatus*. However, this seems more difficult for slow-moving reptiles such as *P. orbiculare* or *Thamnophis* sp., which were often found in bad physical conditions, e.g., slower than normal, dehydrated, and stained with ash.

Table 3. Number of dead and live reptiles, and density of carcasses (total and mean with standard deviation) found during the dry seasons of 2021 and 2022.

2021	Dead	Alive	Total	Dead/ha
Barisia imbricata (Anguidae)	8	4	12	0.07 (0.12 ± 0.30)
Conopsis lineata (Colubridae)	2	2	4	0.02 (0.22 ± 0.86)
Crotalus triseriatus (Viperidae)	0	4	4	0.00
Phrynosoma orbiculare (Phrynosomatidae)	20	24 (4 injured)	44	0.17 (0.30 ± 0.51)
Sceloporus grammicus (Phrynosomatidae)	0	1	1	0.00
Sceloporus torquatus (Phrynosomatidae)	9	61	70	0.07 (0.12 ± 0.21)
Thamnophis sp. (Colubridae)	19	15	34	0.16 (0.84 ± 3.05)
TOTAL	**58**	**111**	**169**	**0.48 (1.60 ± 2.99)**
2022	**Dead**	**Alive**	**Total**	**Dead/ha**
Barisia imbricata (Anguidae)	2	2	4	0.07 (0.05 ± 0.11)
Conopsis lineata (Colubridae)	0	2	2	0.00
Crotalus triseriatus (Viperidae)	0	1	1	0.00
Phrynosoma orbiculare (Phrynosomatidae)	4	11 (2 injured)	15	0.14 (0.13 ± 0.09)
Sceloporus grammicus (Phrynosomatidae)	0	0	0	0.00
Sceloporus torquatus (Phrynosomatidae)	3	5	8	0.10 (0.08 ± 0.16)
Thamnophis sp. (Colubridae)	2	1 (injured)	3	0.07 (0.05 ± 0.11)
TOTAL	**11**	**22**	**33**	**0.38 (0.31 ± 0.27)**

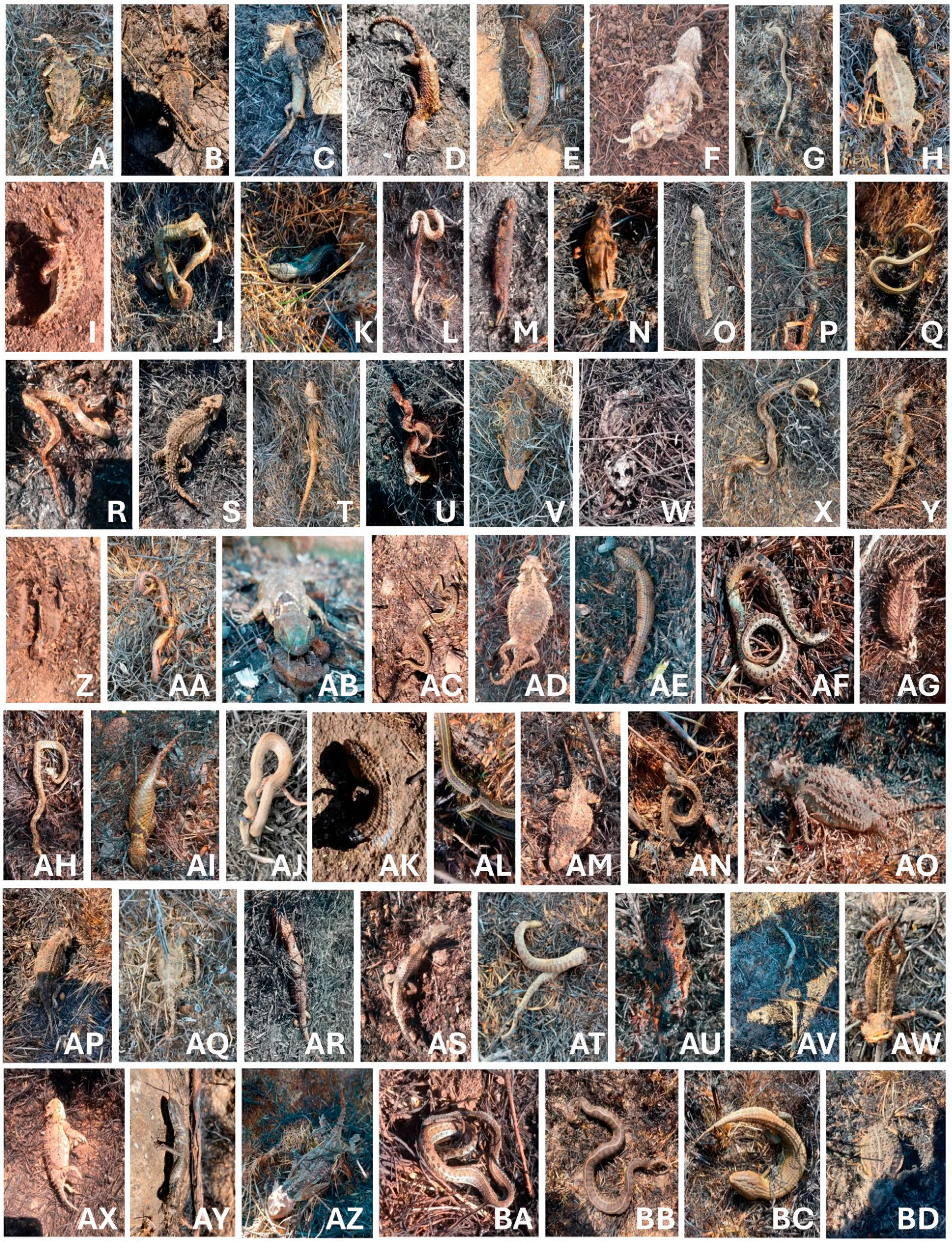

Figure 2. Representative pictures of carcasses found in burned areas in 2021 and 2022. Each picture corresponds to a different individual. The letters A, B, F, H, I, N, S, V, W, Z, AD, AG, AM, AO, AP, AQ, AX, AZ, and BD correspond to *P. orbiculare*; the letters C, E, K, M, O, AE, AK, AR, and BC correspond to *B. imbricata*; the letters D, T, Y, AB, AI, AS, AU, AW, and AY correspond to *S. torquatus*; the letters J, L, P, Q, R, U, X, AA, AC, AF, AH, AL, AN, AT, AV, BA, and BB correspond to *Thamnophis* sp.; and the letters G and AJ correspond to *C. lineata*.

Figure 3. Enlarged pictures shown in Fig. 2 and referenced in the text. The letter W corresponds to a completely calcinated *Phrynosoma orbiculare* that fell apart when we took it. The letter AH corresponds to *Thamnophis scalaris*, almost intact in the middle of a burned surface. The head up suggests death by asphyxia. The letter Q corresponds to *Thamnophis eques* slightly burned above a hole, whereas the letter K corresponds to *Barisia imbricata* slightly burned with half of its body inside a burrow.

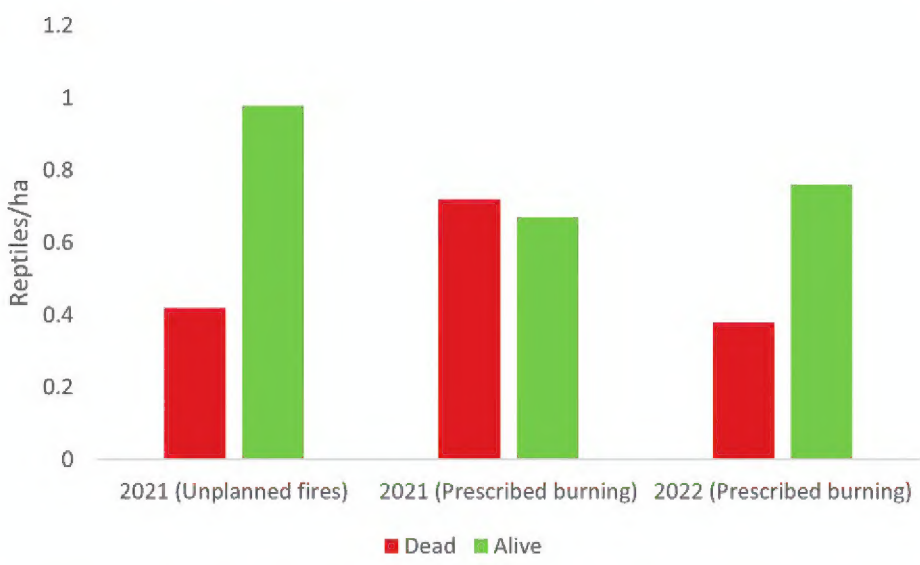

Figure 4. Individuals per hectare found dead and alive in 2021 unplanned fires, 2021 prescribed fires, and 2022 prescribed fires.

Mortality densities

The density of dead reptiles found in our study area is lower than that of other studies, such as in the Pantanal wetland in Brazil, where Tomas et al. (2021) estimated 2.48 dead small reptiles/ha—a value described as astonishing by the authors—and Lapalala wilderness, South Africa (7.77 dead reptiles/ha; Jordaan et al. 2019). Nevertheless, the biodiversity in the PESM is much lower than the biodiversity at these study sites. For example, the Pantanal is the largest wetland in the world, with 113 reptile species reported (including more than 30 species of snakes; Alho 2008), whereas the PESM is a small natural protected area (1,255 hectares) with a low level of protection, situated within a densely populated city and heavily impacted by anthropogenic activities (exotic forest plantations, water pollution, illegal garbage dumps). In the context of lower and more vulnerable biodiversity, the mortality densities found at our study site may alert us to the serious risk that anthropogenic fires can pose to native herpetofauna in fragile ecosystems. At least, our findings contrast with those of several studies that report direct fire-induced mortality in reptiles as rare, negligible, or nonexistent (Costa et al. 2013; Harper et al. 2016; Greenberg et al. 2018; Certini et al. 2021; Jolly et al.

2022). Our findings are rather in line with studies that have already warned about the impacts of fire on reptile populations (Popgeorgiev 2008; Smith et al. 2012; Abom and Schwarzkopf 2016; Jordaan et al. 2019, 2020; Santos et al. 2022; Ballouard et al. 2023) and on vertebrates in general (Berlinck et al. 2021; Tomas et al. 2021).

Detection of individuals

We consider that the mortality densities obtained can be highly underestimated: carcasses are difficult to detect within a burned area, some may be covered by ashes, and some may have been completely calcined (Fig. 3). Some initial survivors, especially those that were injured, may have died after the survey due to wounds or indirect fire effects, and some animals may have died underground or in other refugia; inhalation of hot or toxic gasses produced by fire has been suggested as a source of mortality for snakes that have fled underground (Durbian 2006), making the mortality of these animals nearly impossible to determine. Additionally, surveys were conducted by area (searching across the entire area in a zigzag pattern) rather than by transect, which leaves the possibility that some sites in the largest burned areas were not surveyed. Moreover, it was not always possible to sample the areas during the first week after the fire, extending into the second and, in some cases, the third week; thus, some carcasses may have been eaten by predators/scavengers. For example, Ballouard et al. (2023) reported the disappearance of 20% of carcasses during the second week after a fire. Thus, the overall impact on reptile communities should be considered higher than our counts. Even if mortality by fire has been underestimated in our study, our results still show the major deleterious effects of fire on the reptile community of the PESM.

Mortality rates among species

Phrynosoma orbiculare was the most common carcass found. The high number of carcasses can be attributed to the abundance of this species in certain areas of the natural protected area and its slow movement (Presch 1969), which makes it vulnerable to fire. Fair and Henke (1997) also expressed concerns about fire-induced mortality in Texas horned lizards (*Phrynosoma cornutum*), and other slow-moving lizard species, such as the Australian thorny devil (*Moloch horridus*), have also been reported dead after fire (Smith et al. 2012). The density of *P. orbiculare* carcasses found in 2021 (0.17 ind./ha, mean = 0.30 ind./ha ± 0.51) is similar to that reported for other slow-moving species, such as *Testudo hermanni* (0.19 ind./ha) (Ballouard et al. 2023). In contrast, *S. torquatus*, another lizard of the Phrynosomatidae family that is similar in size and very abundant in the area, experienced markedly lower mortality. This is likely due to its greater speed and ability as a lapidicolous species, enabling it to climb logs, shrubs, agaves, and rock walls.

Thamnophis sp. carcasses were also among the most commonly found. Although they can retreat to underground burrows, ground-dwelling and slow-moving species are more vulnerable to fire than lapidicolous species. Other studies have reported severe fire-induced mortality in snakes (Durbian 2006; Lyet et al. 2009; Cross 2015). For example, small snakes represented 55% of the dead vertebrates recorded in wildfires that hit the Brazilian portion of the Pantanal wetland in 2020 (Tomas et al. 2021). *Thamnophis* sp. were the only species among which some dead individuals (three) were found without signs of burns. These individuals also did not exhibit any other signs of visible damage and were found on a completely burned surface (Fig. 3). A study carried out in the PESM reported that *T. scalaris* can retreat in underground hollows or burrows deeper than one meter (Mundo-Hernández et al. 2017), and studies with better-known *Thamnophis* species from other regions, such as *T. sirtalis*, reported that they use two-meter-deep hollows (Shine and Mason 2004). The dead *Thamnophis* individuals found in our study with no visible burns may have been below ground during the fire and came out after the flames consumed the vegetation and passed by; however, they probably died as a consequence of smoke inhalation or noxious gas inhalation. This is consistent with the findings of other studies on the effects of fire on fossorial reptiles, where dead reptiles were found on the soil surface, some in positions suggesting these animals attempted to reach the surface (Jordaan et al. 2020). Such observations have led to the hypothesis that burrowing reptiles are not necessarily protected from fire effects (Engstrom 2010). Deaths by smoke inhalation and inhalation of noxious gases produced during burning in association with anoxia have been reported for snakes (Durbian 2006; Lyet et al. 2009; Jordaan and Steyl 2023) and other reptiles (Jordaan et al. 2019; Jordaan and Steyl 2023). Finally, we found a relatively high number of *B. imbricata* carcasses (10), considering that this species is not very abundant in the PESM, which suggests that this ground-dwelling species may also be highly vulnerable to fire.

Differences between sampled burned sites

Site 13 had the highest number of dead reptiles (20 individuals). The fire was caused by stubble burning, which went out of control. However, the mortality density at this site was lower than in other sites. This may be because the zigzag survey pattern is insufficiently thorough for such a large area. The highest mortality density was found at site 8, which was a firebreak located alongside a canal that carries water during the wet season. We found three *Thamnophis* sp. carcasses in this small firebreak. This may be due to the greater density of *Thamnophis* near the canal than in other areas without water bodies. We found no relationship between carcass density and fire shape. This could be attributed to

the limitations of the simple measure (area/perimeter), which does not account for landscape elements such as the presence and distribution of rocky areas, agave plants, and other potential refuges. These elements could serve as more effective indicators for explaining variations in mortality density across sites. For example, Hale et al. (2022) and Robinson et al. (2013) found that the presence of refugia in burned areas is a key factor that explains wildlife resistance to fire. Other variables not measured in this study, such as wind direction and speed during the fire, as well as the severity of the fire, are likely to have also impacted mortality rates at each study site. Slower and lower-intensity fires would have provided greater opportunities for animal survival.

Prescribed burning vs. unplanned fires

Prescribed burning is the intentional use of fire under specific environmental conditions (e.g., during the dormant season) to achieve various land management goals. It has been reported as an appropriate management tool to benefit herpetofauna by restoring a historical mosaic of successional stages (Russell et al. 1999) and by generating more open habitats with greater insolation (Matthews et al. 2010). However, our study questions these views. We report no statistically significant differences in the densities of dead individuals between unplanned and prescribed burned areas. This may be because, in our study, both prescribed and unplanned fires occurred during the same season (the fire-prone season), and it is likely that the fire severities were similar. As evidence, an individual of *P. orbiculare* was found completely calcinated in a prescribed burned area.

Some studies suggest that prescribed fire effects on herpetofauna can be reduced by conducting burning practices during winter, when many terrestrial herpetofaunal species are inactive and are likely below ground or otherwise insulated from high temperatures and the potential desiccating effects of fire (Harper et al. 2016). However, in our study, all the carcasses found in the prescribed burned areas were from fires conducted during the cold and dry seasons (January and February). We must consider that although the climate of our study site is classified as temperate, it exhibits important differences compared to temperate climates at higher latitudes. At night, temperatures can drop below zero degrees Celsius, but during the hottest hours of the day, they can reach more than twenty degrees. Fires occurring when reptiles are less active can cause less mortality only if inactive reptiles are protected from fire. At our study site, reptiles are less active during the cold and dry seasons but are not completely inactive, and they are not necessarily hidden at a sufficient depth as in colder climates. For example, when *P. orbiculare* is less active, it shelters under bunchgrass or leaf litter (Gómez-Benítez et al. 2021), increasing its vulnerability to fire compared to when it is active (e.g., in areas with less vegetation coverage, looking for ants).

Management implications

On the basis of our findings, we seriously question prescribed burning practices in the PESM and in similar ecosystems of the region, e.g., grasslands that share a similar reptile community composition. Prescribed burning has been carried out in the same grassland areas of the PESM during consecutive years, causing deaths in the same reptile populations, with the main objective of preserving areas with planted trees that are not native and, moreover, fire-dependent (which is related to the promotion of tree planting in the country as a "green" policy that does not adhere to ecological criteria, stemming from the misconception that grasslands or shrublands are less important than forests). Whelan (2002) affirms that populations of many species are less threatened by a single high-intensity fire event than by a sequence of lower-intensity fires in close succession. In the study by Abom and Schwarzkopf (2016), reptile numbers in native grass were found to decline after fire and failed to return to previous numbers with revegetation even in extremely fire-prone, often-burned environments, suggesting that longer periods without burning may be beneficial to reptile assemblages. Furthermore, annual fires disrupt the natural succession of vegetation and hinder regrowth, even for fire-adapted species such as native *Quercus* populations (Trejo 2008).

In the PESM, unplanned fires (e.g., man-made illegal and accidental burns) continue to occur every year despite prescribed burning practices. Unplanned fires are related to a variety of factors, including the use of fire in agriculture and grazing, the practice of trash burning in the vicinity of precarious settlements, the presence of remaining campfires, and the disposal of cigarettes. The practice of systematic 'weed clearance' in natural and semi-natural areas around settlements has led to burning every vacant lot, roadside, and land between crops every year, and is likely the main contributor to unplanned fires in the region, as these fires often spread out of control. Both planned and unplanned fires may have a cumulative impact on the most affected reptile species, such as *P. orbiculare* (which is an endangered species in Mexico), *Thamnophis* sp. (which also suffer from direct killing by humans), and *B. imbricata* (which is less abundant in the natural protected area). The recovery of these populations will also be hindered by the fact that the PESM is a small natural protected area surrounded by urbanized land and agricultural fields and disconnected from other natural environments. This situation can potentially affect reptile diversity and the community composition of PESM in the long term.

Stopping prescribed burns as part of the PESM management program is important. However, if we aim to protect these reptile species, it is also necessary to halt the unplanned fires that have been observed to burn a greater proportion of the natural protected area annually.

More systematic surveys that quantify direct fire-induced reptile mortality and reptile densities before and after the fires in the PESM and similar ecosystems in the

region may allow for better direct comparisons of mortality rates and the direct impacts of fires on reptile populations. With the objective of lowering the occurrence and extent of anthropogenic fires and preserving the native biodiversity in the PESM, we suggest several actions be considered. 1) Maintaining a well-distributed bike path network in the area, as bike paths can act as firebreaks. 2) Rotating the existing small-scale livestock farming, as it can reduce fuel accumulation while reducing grazing pressure in specific areas of the PESM. 3) Progressively replacing exotic and flammable plantations of *Pinus radiata* and eucalyptus with native vegetation, as the resins of these commonly planted species are highly flammable, increasing the likelihood and rate of wildfire propagation (McWethy et al. 2018). 4) Implementing a collaborative network and awareness campaign to enhance vigilance across multiple communities during the dry season. 5) Restoring biophysical structures in the landscape, such as agaves, which serve as refuges for some reptiles during fires. 6) Conducting active postfire searches for reptiles, pouring some water over them, and relocating survivors to safer areas outside the burned zone.

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References

Abom R, Schwarzkopf L (2016) Short-term responses of reptile assemblages to fire in native and weedy tropical savannah. Global Ecology and Conservation 6: 58–66. https://doi.org/10.1016/j.gecco.2016.02.002

Alho CJR (2008) Biodiversity of the Pantanal: response to seasonal flooding regime and to environmental degradation. Brazilian Journal of Biology 68: 957–966. https://doi.org/10.1590/S1519-69842008000500005

Ballouard JM, Afériat M, Gillet G, Daneluzzi A, Yvin M, Garnier E, Levasseur R, Moreaux L, Delorme O, Guicheteau D, Caron S (2023) Impact d'un incendie en fonction de l'habitat sur la population de tortues d'Hermann Testudo hermanni hermanni de la Réserve Naturelle Nationale de la Plaine des Maures. Bulletin de la Société Herpétologique de France 183: 1–17. https://doi.org/10.48716/bullshf.183-2

Berlinck CN, Lima LH, Pereira AM, Carvalho Jr EA, Paula RC, Thomas WM, Morato RG (2021) The Pantanal is on fire and only a sustainable agenda can save the largest wetland in the world. Brazilian Journal of Biology 82: e244200. https://doi.org/10.1590/1519-6984.244200

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution 20(7): 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bowman DM, Balch J, Artaxo P, Bond WJ, Cochrane MA, D'antonio CM, DeFries R, Johnston FH, Keeley JE, Krawchuk MA, Kull CA (2011) The human dimension of fire regimes on Earth. Journal of Biogeography 38(12): 2223–2236. https://doi.org/10.1111/j.1365-2699.2011.02595.x

Bowman DM, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP, Johnston FH (2009) Fire in the Earth system. Science 324(5926): 481–484. https://doi.org/10.1126/science.1163886

Bowman DM, Kolden CA, Abatzoglou JT, Johnston FH, van der Werf GR, Flannigan M (2020) Vegetation fires in the Anthropocene. Nature Reviews Earth and Environment 1(10): 500–515. https://doi.org/10.1038/s43017-020-0085-3

Bury RB (2004) Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests. Conservation Biology 18(4): 968–975. https://doi.org/10.1111/j.1523-1739.2004.00522.x

Certini G, Moya D, Lucas-Borja ME, Mastrolonardo G (2021) The impact of fire on soil-dwelling biota: A review. Forest Ecology and Management 488: 118989. https://doi.org/10.1016/j.foreco.2021.118989

Conner LM, Castleberry SB, Derrick AM (2011) Effects of mesopredators and prescribed fire on hispid cotton rat survival and cause-specific mortality. The Journal of Wildlife Management 75(4): 938–944. https://doi.org/10.1002/jwmg.110

Costa BM, Pantoja DL, Vianna MCM, Colli GR (2013) Direct and short-term effects of fire on lizard assemblages from a Neotropical savanna hotspot. Journal of Herpetology 47(3): 502–510. https://doi.org/10.1670/12-043

Cross MD (2015) Multiscale responses of eastern massasauga rattlesnakes (*Sistrurus catenatus*) to prescribed fire. The American Midland Naturalist 173(2): 346–362. https://doi.org/10.1674/amid-173-02-346-362.1

Duane A, Castellnou M, Brotons L (2021) Toward a comprehensive look at global drivers of novel extreme wildfire events. Climatic Change 165(3): 1–21. https://doi.org/10.1007/s10584-021-03066-4

Durbian FE (2006) Effects of mowing and summer burning on the massasauga (*Sistrurus catenatus*). The American Midland Naturalist 155(2): 329–334. https://doi.org/10.1674/0003-0031(2006)155[329:EOMASB]2.0.CO;2

Engstrom RT (2010) First-order fire effects on animals: review and recommendations. Fire Ecology 6: 115–130. https://doi.org/10.4996/fireecology.0601115

Fair WS, Henke SE (1997) Effects of habitat manipulations on Texas horned lizards and their prey. The Journal of Wildlife Management 1366–1370. https://doi.org/10.2307/3802139

Ferreira CC, Santos X, Carretero, MA (2016a) Does ecophysiology mediate reptile responses to fire regimes? Evidence from Iberian lizards. PeerJ 4: e2107. https://doi.org/10.7717/peerj.2107

Ferreira D, Mateus C, Santos X (2016b) Responses of reptiles to fire in transition zones are mediated by bioregion affinity of species. Biodiversity and Conservation 25: 1543–1557. https://doi.org/10.1007/s10531-016-1137-3

Floyd TM, Russell KR, Moorman CE, Van Lear DH, Guynn Jr DC, Lanham JD (2002) Effects of prescribed fire on herpetofauna within hardwood forests of the upper piedmont of South Carolina: a preliminary analysis. In: Outcalt KW (Ed.) Proceedings of the 11th Biennial Southern Research Conference. U.S. Forest Service General Technical Report SRS-48, Asheville, NC, 123–127.

Ford WM, Menzel MA, McGill DW, Laerm J, McCay TS (1999) Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. Forest Ecology and Management 114(2–3): 233–243. https://doi.org/10.1016/S0378-1127(98)00354-5

Garcia LC, Szabo JK, de Oliveira Roque F, Pereira AD, da Cunha CN, Damasceno-Júnior GA, Morato RG, Tomas WM, Libonati R, Ribeiro DB (2021) Record-breaking wildfires in the world's largest continuous tropical wetland: integrative fire management is urgently needed for both biodiversity and humans. Journal of Environmental Management 293: 112870. https://doi.org/10.1016/j.jenvman.2021.112870

Gobierno del Estado de México (1976) Decreto del Ejecutivo del Estado por el que se crea el parque estatal denominado "Sierra Morelos" ubicado en el municipio de Toluca, Estado de México. Gaceta del Gobierno 13: 1–14.

Gobierno del Estado de México (1981) Decreto del Ejecutivo del Estado por el que se integra al parque estatal "Sierra Morelos", la zona montañosa ubicada al norte del Valle de Toluca en el Municipio de Toluca, Estado de México. Gaceta del Gobierno 33: 1–4.

Gobierno del Estado de México (2013) Resumen ejecutivo del programa de conservación y manejo del parque estatal "Sierra Morelos". Gaceta del Gobierno 45: 1–32.

Gómez-Benítez A, Loza CAM, Rodríguez ASV, Rheubert JL, Gallegos OH (2021) Spatial-Temporal Activity Patterns of the Mexican Plateau Horned Lizard in a Natural Protected Area. Journal of Herpetology 55(3): 271–278. https://doi.org/10.1670/20-037

Greenberg CH, Seiboldt T, Keyser TL, McNab WH, Scott P, Bush J, Moorman CE (2018) Reptile and amphibian response to season of burn in an upland hardwood forest. Forest Ecology and Management 409: 808–816. https://doi.org/10.1016/j.foreco.2017.12.016

Greenberg CH, Waldrop TA (2008) Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. Forest Ecology and Management 255(7): 2883–2893. https://doi.org/10.1016/j.foreco.2008.01.064

Hale S, Mendoza L, Yeatman T, Cooke R, Doherty T, Nimmo D, White JG (2022) Evidence that post-fire recovery of small mammals occurs primarily via in situ survival. Diversity and Distributions 28(3): 404–416. https://doi.org/10.1111/ddi.13283

Harper CA, Ford WM, Lashley MA, Moorman CE, Stambaugh MC (2016) Fire effects on wildlife in the Central Hardwoods and Appalachian regions, USA. Fire Ecology 12: 127–159. https://doi.org/10.4996/fireecology.1202127

He T, Lamont BB, Pausas JG (2019) Fire as a key driver of Earth's biodiversity. Biological Reviews 94(6): 1983–2010. https://doi.org/10.1111/brv.12544

Hernández-Navarrete (2018) Edad y crecimiento corporal de Phrynosoma orbiculare (Squamata: Phrynosomatidae). Bachelor's thesis, Universidad Autónoma del Estado de México, Toluca, Mexico.

Jolly CJ, Dickman CR, Doherty TS, van Eeden LM, Geary WL, Legge SM, Woinarski JC, Nimmo DG (2022) Animal mortality during fire. Global Change Biology 28: 2053–2065. https://doi.org/10.1111/gcb.16044

Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DM (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications 6(1): 7537. https://doi.org/10.1038/ncomms8537

Jordaan PR, Steyl JC (2023) Fire-induced mortality and associated pathologies across functional reptile groups in relation to fire behavior. Herpetology Notes 16: 315–321.

Jordaan PR, Steyl JC, Hanekom CC, Combrink X (2020) Fire-associated reptile mortality in Tembe Elephant Park, South Africa. Fire Ecology 16(1): 1–6. https://doi.org/10.1186/s42408-019-0066-4

Jordaan PR, van der Goot AC, Muller HP, Steyl JCA (2019) Fire-induced reptile mortality following a management burn on Lapalala Wilderness (Limpopo Province, South Africa) with notes on the mechanisms of mortality. Herpetology Notes 12: 1173–1177.

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA (2011) Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science 16: 406–411. https://doi.org/10.1016/j.tplants.2011.04.002

Kelly LT, Giljohann KM, Duane A, Aquilué N, Archibald S, Batllori E, Bennett AF, Buckland ST, Canelles Q, Clarke MF, Fortin MJ (2020) Fire and biodiversity in the Anthropocene. Science 370(6519): eabb0355. https://doi.org/10.1126/science.abb0355

Langford GJ, Borden JA, Major CS, Nelson DH (2007) Southern Mississippi pine savanna. Herpetological Conservation and Biology 2(2): 135–143.

Leahy L, Legge SM, Tuft K, McGregor HW, Barmuta LA, Jones ME, Johnson CN (2016) Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. Wildlife Research 42(8): 705–716. https://doi.org/10.1071/WR15011

Legge S, Murphy S, Heathcote J, Flaxman E, Augusteyn J, Crossman M (2008) The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. Wildlife Research 35(1): 33–43. https://doi.org/10.1071/WR07016

Lyet A, Cheylan M, Prodon R, Besnard A (2009) Prescribed fire and conservation of a threatened mountain grassland specialist: a capture–recapture study on the Orsini's viper in the French alps. Animal Conservation 12(3): 238–248. https://doi.org/10.1111/j.1469-1795.2009.00245.x

Manjarrez J, Contreras-Garduño J, Janczur MK (2014) Sexual size dimorphism, diet and reproduction in the Mexican garter snake, *Thamnophis eques*. Herpetological Conservation and Biology 9(1): 163–169.

Manjarrez J, Venegas-Barrera CS, García-Guadarrama T (2007) Ecology of the Mexican alpine blotched garter snake (*Thamnophis scalaris*). The Southwestern Naturalist 52(2): 258–262. https://doi.org/10.1894/0038-4909(2007)52[258:EOTMAB]2.0.CO;2

Matthews CE, Moorman CE, Greenberg CH, Waldrop TA (2010) Response of reptiles and amphibians to repeated fuel reduction treatments. The Journal of Wildlife Management 74(6): 1301–1310. https://doi.org/10.1111/j.1937-2817.2010.tb01251.x

McKenzie D, Gedalof ZE, Peterson DL, Mote P (2004) Climatic change, wildfire, and conservation. Conservation Biology 18(4): 890–902. https://doi.org/10.1111/j.1523-1739.2004.00492.x

McLauchlan KK, Higuera PE, Miesel J, Rogers BM, Schweitzer J, Shuman JK, Tepley AJ, Varner JM, Veblen TT, Adalsteinsson SA, Balch JK (2020) Fire as a fundamental ecological process: Research advances and frontiers. Journal of Ecology 108(5): 2047–2069. https://doi.org/10.1111/1365-2745.13403

McLeod RF, Gates JE (1998) Response of herpetofaunal communities to forest cutting and burning at Chesapeake farms, Maryland. The American Midland Naturalist 139(1): 164–177. https://doi.org/10.1674/0003-0031(1998)139[0164:ROHCTF]2.0.CO;2

McWethy DB, Pauchard A, García RA, Holz A, González ME, Veblen TT, Stahl J, Currey B (2018) Landscape drivers of recent fire activity (2001–2017) in south-central Chile. PLOS ONE 13(8): e0201195. https://doi.org/10.1371/journal.pone.0201195

Means DB, Campbell HW (1981) Effects of prescribed burning on amphibians and reptiles. In Prescribed fire and wildlife in southern forests: Proceedings of a Symposium, 6–8.

Mundo-Hernández V, Domínguez-Vega H, Gómez-Ortiz Y, Rubio-Blanco T, Soria-Díaz L, Manjarrez J (2017). Hibernation refuge of *Thamnophis scalaris* Cope, 1861, in Central Mexico. Herpetozoa 29: 198–200.

Nimmo DG, Carthey AJ, Jolly CJ, Blumstein DT (2021) Welcome to the Pyrocene: Animal survival in the age of megafire. Global Change Biology 27(22): 5684–5693. https://doi.org/10.1111/gcb.15834

Niño-Gutiérrez NS, Melo-Gallegos C, Sierra-Domínguez G (2007) Diagnóstico actual de los recursos naturales del parque estatal "Sierra Morelos", Estado de México. Revista Producción Animal en Zonas Áridas y Semiáridas. Universidad Autónoma de Chihuahua 108: 582–586.

Olvera-Viscaino D (2018) Gobernanza ambiental en el parque estatal Sierra Morelos. Bachelor Thesis, Universidad Autónoma del Estado de México.

Ortiz MF, De Oca ANM, Ugarte IHS (2001) Diet and reproductive biology of the viviparous lizard *Sceloporus torquatus torquatus* (Squamata: Phrynosomatidae). Journal of Herpetology 104–112. https://doi.org/10.2307/1566029

Parr CL, Andersen AN (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conservation Biology 20(6): 1610–1619. https://doi.org/10.1111/j.1523-1739.2006.00492.x

Pausas JG, Keeley JE (2009) A burning story: the role of fire in the history of life. BioScience 59(7): 593–601. https://doi.org/10.1525/bio.2009.59.7.10

Pausas JG, Parr CL (2018) Toward an understanding of the evolutionary role of fire in animals. Ecology and Evolution 32: 113–125. https://doi.org/10.1007/s10682-018-9927-6

Popgeorgiev GS, Kornilev YV (2009) Effects of a High Intensity Fire on the Abundance and Diversity of Reptiles in the Eastern Rhodopes Mountains, Southeastern Bulgaria. Ecologia Balkanica 1: 41.

Popgeorgiev G (2008) The effects of a large-scale fire on the demographic structure of a population of Hermann's (*Testudo hermanni boettgeri* Mojsisovics, 1889) and Spur-thighed (*Testudo graeca ibera* Pallas, 1814) tortoises in Eastern Rhodopes Mountains, Bulgaria. Historia Naturalis Bulgarica 19: 115–127.

Presch W (1969) Evolutionary osteology and relationships of the horned lizard genus Phrynosoma. Copeia 250–275. https://doi.org/10.2307/1442073

Reguera S, Santos X, Feriche M, Mociño-Deloya E, Setser K, Pleguezuelos JM (2011). Diet and energetic constraints of an earthworm specialist, the Mesa Central Blotched Garter Snake (*Thamnophis scaliger*). Canadian Journal of Zoology 89(12): 1178–1187. https://doi.org/10.1139/z11-096

Robinson NM, Leonard SW, Ritchie EG, Bassett M, Chia EK, Buckingham S, Gibb H, Bennett AF, Clarke MF (2013) Refuges for fauna in fire-prone landscapes: their ecological function and importance. Journal of Applied Ecology 50(6): 1321–1329. https://doi.org/10.1111/1365-2664.12153

Rubio-Blanco T, Martínez-Díaz-González R, Heredia-Bobadilla RL, Guido-Patiño JC, Arenas S, Caballero-Viñas C, Manjarrez J, Domínguez-Vega H, Gómez-Ortiz Y, Ramos-Olguin AD, Sunny A (2024) Predicting the effects of climate and land use changes on small rattlesnakes in central Mexico: Insights for conservation planning. Journal for Nature Conservation 79: 126607. https://doi.org/10.1016/j.jnc.2024.126607

Russell KR, Van Lear DH, Guynn Jr DC (1999) Prescribed fire effects on herpetofauna: review and management implications. Wildlife Society Bulletin 374–384. https://www.jstor.org/stable/3783904

Santos JL,Sitters H, Keith DA, Geary WL, Tingley R, Kelly LT (2022) A demographic framework for understanding fire-driven reptile declines in the 'land of the lizards'. Global Ecology and Biogeography 31(10): 2105–2119. https://doi.org/10.1111/geb.13520

Santos X, Badiane A, Matos C (2016) Contrasts in short-and long-term responses of Mediterranean reptile species to fire and habitat structure. Oecologia 180(1): 205–216. https://doi.org/10.1007/s00442-015-3453-9

Santos X, Belliure J, Gonçalves JF, Pausas JG (2021) Resilience of reptiles to megafires. Ecological Applications 32(2): e2518. https://doi.org/10.1002/eap.2518

Santos X, Cheylan M (2013) Taxonomic and functional response of a Mediterranean reptile assemblage to a repeated fire regime. Biological Conservation 168: 90–98. https://doi.org/10.1016/j.biocon.2013.09.008

Santos X, Poquet JM (2010) Ecological succession and habitat attributes affect the postfire response of a Mediterranean reptile community. European Journal of Wildlife Research 56: 895–905. https://doi.org/10.1007/s10344-010-0387-8

Seager R, Ting M, Davis M, Cane M, Naik N, Nakamura J, Li C, Cook E, Stahle DW (2009) Mexican drought: an observational modeling and tree ring study of variability and climate change. Atmósfera 22(1): 1–31.

SEMARNAT (2010) Norma Oficial Mexicana NOM-059-SEMARNAT-2010. Protección ambiental, especies nativas de flora y fauna silvestres de México, categorías de riesgo y especificaciones para su inclusión, exclusión o cambio, y lista de especies en riesgo. Diario Oficial de la Federación, 30 de diciembre de 2010, Segunda Sección. Ciudad de México, México.

Servicio Meteorológico Nacional (2021) Normales Climatológicas. Estado de México. https://smn.conagua.gob.mx/tools/RESOURCES/Normales_Climatologicas/Normales9120/mex/nor9120_15203.TXT

Shine R, Mason RT (2004) Patterns of mortality in a cold-climate population of garter snakes (*Thamnophis sirtalis parietalis*). Biological Conservation 120(2): 201–210. https://doi.org/10.1016/j.biocon.2004.02.014

Sierra-Domínguez G, Flores-Olvera P, Pérez-Ramírez CA (2018) Factor de cambio antropogénico detectado en los ecosistemas del parque estatal Sierra Morelos: el crecimiento poblacional. En: Vulnerabilidad, resiliencia y ordenamiento territorial. Ed: Juárez MVS, Hoyos G, Castañeda GS.

Smith AL (2018) Successional changes in trophic interactions support a mechanistic model of postfire population dynamics. Oecologia 186(1): 129–139. https://doi.org/10.1007/s00442-017-4016-z

Sunny A, Gandarilla-Aizpuro FJ, Monroy-Vilchis O, Zarco-Gonzalez MM (2019) Potential distribution and habitat connectivity of *Crotalus triseriatus* in Central Mexico. Herpetozoa 32: 139–148. https://doi.org/10.3897/herpetozoa.32.e36361

Sunny A, González-Fernández A, D'Addario M (2017) Potential distribution of the endemic imbricate alligator lizard (*Barisia imbricata imbricata*) in highlands of central Mexico. Amphibia-Reptilia 38(2): 225–231. https://doi.org/10.1163/15685381-00003092

Sunny A, Manjarrez J, Caballero-Viñas C, Bolom-Huet R, Gómez-Ortiz Y, Domínguez-Vega H, Heredia-Bobadilla RL, Torres-Romero EJ, González-Fernández A (2023) Modelling the effects of climate and land-cover changes on the potential distribution and landscape connectivity of three earth snakes (Genus *Conopsis*, Günther 1858) in central Mexico. The Science of Nature 110(6): 52. https://doi.org/10.1007/s00114-023-01880-7

Tomas WM, Berlinck CN, Chiaravalloti RM, Faggioni GP, Strüssmann C, Libonati R, Abrahão CR, do Valle Alvarenga G, de Faria Bacellar AE, de Queiroz Batista FR, Bornato TS (2021) Distance sampling surveys reveal 17 million vertebrates directly killed by the 2020's wildfires in the Pantanal. Brazil Scientific Reports 11(1): 1–8. https://doi.org/10.1038/s41598-021-02844-5

Trejo DAR (2008) Fire regimes, fire ecology, and fire management in Mexico. AMBIO: a Journal of the Human Environment 37(7): 548–556. https://doi.org/10.1579/0044-7447-37.7.548

Valentine LE, Schwarzkopf LIN (2009) Effects of weed-management burning on reptile assemblages in Australian tropical savannas. Conservation Biology 23(1): 103–113. https://doi.org/10.1111/j.1523-1739.2008.01074.x

Whelan RJ (2002) Managing fire regimes for conservation and property protection: an Australian response. Conservation Biology 16(6): 1659–1661. https://doi.org/10.1046/j.1523-1739.2002.02091.x

Woolrich-Piña GA, Smith GR, Martínez-Méndez N, Lemos-Espinal JA, Gadsden-Esparz H (2021) Effects of body temperature on initial bite force in three species of rock-and crevice-dwelling lizards from Mexico. Herpetozoa 34: 163–168. https://doi.org/10.3897/herpetozoa.34.e64040

Supplementary material 1

Historical report of fires and preventive activities in the Sierra Morelos State Park carried out by Probosque

Authors: Andrea González-Fernández, Stephane Couturier, Rodrigo Dotor-Diego, Ricardo Martínez-Díaz-González, Armando Sunny

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Supplementary material 2

Enlarged pictures shown in Fig. 2

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Data type: pdf

Explanation note: Each picture corresponds to a different carcass found in burned areas in 2021 and 2022.

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